Effects of Cattle Grazing on Diversity in Ephemeral Wetlands

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Abstract: *Cattle are usually thought of as a threat to biodiversity. In regions threatened by exotic species invasion and lacking native wild grazers, however, cattle may produce the type of disturbance that helps maintain diverse communities. Across 72 vernal pools, I examined the effect of different grazing treatments (ungrazed, continuously grazed, wet-season grazed and dry-season grazed) on vernal-pool plant and aquatic faunal diversity in the Central Valley of California. After 3 years of treatment, ungrazed pools had 88% higher cover of exotic annual grasses and 47% lower relative cover of native species than pools grazed at historical levels (continuously grazed). Species richness of native plants declined by 25% and aquatic invertebrate richness was 28% lower in the ungrazed compared with the continuously grazed treatments. Release from grazing reduced pool inundation period by 50 to 80%, making it difficult for some vernal-pool endemic species to complete their life cycle. My results show that one should not assume livestock and ranching operations are necessarily damaging to native communities. In my central California study site, grazing helped maintain native plant and aquatic diversity in vernal pools.*

Key Words: biodiversity, grazing, land management, species richness, vernal pools

Efectos del Apacentamiento de Ganado sobre la Diversidad en Humedales Efímeros

Resumen: *Generalmente se piensa que el ganado es una amenaza para la biodiversidad. Sin embargo, en regiones amenazadas por la invasión de especies exóticas y carentes de apacentadores silvestres nativos, el ganado puede producir el tipo de perturbación que ayuda a mantener a diversas comunidades. Examiné el efecto de diferentes tratamientos de apacentamiento (sin apacentamiento, apacentamiento continuo, apacentamiento en época de lluvias y apacentamiento en época de sequía) sobre la diversidad de plantas y fauna acuática en 72 charcos primaverales en el Valle Central de California. Después de tres años de tratamiento, las charcas sin apacentamiento tenían 88% de más cobertura de pastos anuales exóticos y 47% de menos cobertura relativa de especies nativas que charcas con apacentamiento en niveles históricos (apacentados continuamente). La riqueza de especies de plantas nativas declinó en 25% y la riqueza de invertebrados acuáticos fue 28% menor en los tratamientos sin apacentamiento que en los apacentados continuamente. El cese de apacentamiento redujo el período de inundación entre 50 y 80%, haciendo que a algunas especies endémicas de charcos primaverales se les dificultara completar su ciclo de vida. Mis resultados muestran que no se debe asumir que la operación de ganado y de ranchos necesariamente es dañina para las comunidades nativas. En mi sitio de estudio en el centro de California, el apacentamiento ayudó a mantener la diversidad acuática y de plantas nativas en charcos primaverales.*

Palabras Clave: apacentamiento, biodiversidad, charcos primaverales, gestión de tierras, riqueza de especies

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Introduction

Disturbance plays a critical role in maintaining the diversity, structure, and function in many ecological systems (White 1979; Sousa 1984; Hobbs & Huenneke 1992). Grazing is an important widespread disturbance in natural grasslands (McNaughton et al. 1989; Milchunas & Lauenroth 1993; Perevolotsky & Seligman 1998); native herbivores have been extirpated from many grassland ecosystems, however, and replaced with non-native ungulate species. Poorly managed grazing has negatively affected biodiversity in some ecosystems (Painter & Belsky 1993; Fleischner 1994; Freilich et al. 2003), but livestock can also serve as a functional equivalent to large herbivores that historically grazed grasslands and play an essential role in maintaining biodiversity (Collins et al. 1998; Harrison 1999; Maestas et al. 2003).

One might expect grazing to be most beneficial in areas where keystone herbivores have been removed and cannot be reintroduced for practical or economic reasons. In fact in some regions domestic livestock such as cattle may be the only grazer available for the promotion of biodiversity (Knapp et al. 1999). Although a number of studies have recorded higher biodiversity in grazed relative to ungrazed systems (Noy-Meir et al. 1989; Harrison 1999; Hayes & Holl 2003) and have quantified that grazing can effectively control invasive species (Stohlgren et al. 1999; DiTomaso 2000), none has sampled both plant and aquatic diversity in the same system, quantified invasive species, and taken measurements that allow one to consider altered hydrology. In other words, few grazing studies consider other measures of ecosystem response to grazing treatments beyond biodiversity of a single trophic level.

Vernal pools occur throughout California's Central Valley grasslands, where the soils restrict water percolation. These seasonal wetlands fill with water in the winter rainy season, dry down in the spring as rainfall decreases and temperatures rise, and remain desiccated throughout the hot, dry summer. These extreme conditions create a unique ecosystem that harbors high species diversity and endemism: more than 100 vascular plant species and more than 34 crustacean species (King et al. 1996; Keeley & Zedler 1998). Consequently, vernal pools have become a target for conservation organizations and are the sort of target that often prompts conservationists to think they need to remove cattle from the land (Barry 1998; Griggs 2000). Vernal-pool habitats are disappearing rapidly in California. In the last 20 years more than one-third of the vernal-pool habitat in Sacramento County alone has been lost to development (Holland 1998). It is a matter of urgency that the last remaining vernal pools be protected, and the science informing these conservation efforts has lacked an experimental foundation. A major controversy surrounding the conservation of vernal pools concerns grazing. Some argue we need to remove cattle from the vicinity of these threatened habitats, and others argue cattle should be used to manage vernal-pool grasslands. In fact, cattle grazing was implicated as a major contributing factor to the decline of four vernal-pool crustaceans listed under the U.S. Endangered Species Act (USFWS 1994) with little to no supporting scientific data.

I controlled grazing timing in vernal-pool grasslands in California's Central Valley to determine the effects of grazing on native plant and aquatic faunal diversity. I hypothesized that removing grazing would negatively impact plant species diversity but would have either neutral or positive effects on aquatic invertebrate and vertebrate diversity. My experiments involved natural vernal pools across two different soil types and a wide range of vernal pool sizes and depths. I removed grazing either completely or seasonally from groups of pools and compared the response of plant species cover and diversity, pool hydroperiod, soil compaction, and aquatic invertebrate diversity to pools grazed at historical levels.

Methods

Study Site

I conducted my experiments on a 5000-ha parcel of land in eastern Sacramento County, California (USA) (38°38′N, 121°02′W; elevation, 75 m). The climate of this region is Mediterranean, with average annual rainfall of 56 cm occurring between October and May. Less than 2 cm of rain falls from June through September.

The area is flat with low-lying hills that rise in elevation from 50 to 160 m. Vernal pools occur in the lower, flatter areas and are abundant on approximately one-third of the area. The site has been grazed by cattle for the past 100 or more years. Cattle graze the entire site each year from approximately October through June at a stocking rate of 1 animal unit (cow-calf pair) per 2.4 ha.

Experimental Design

In 2000 I selected 24 groups of pools (4 treatments × 6 blocks) for use in this study based on soil maps, aerial photographs, and available geographic information system mapping of vernal pool occurrence. Each treatment plot contained three nested pools (24 treatment plots × 3 pools = 72 pools) of varying sizes (range: 70–1130 m^2, mean: 252 m^2) and shapes. I stratified the treatments across two major geologic formations occurring on the ranch (the Laguna and Valley Springs formations) and randomly assigned treatments to the four plots within each block. Three of the blocks (12 plots) were located on the Valley Springs formation and the other three on the Laguna formation.

I applied four grazing treatments to the plots during the 2000–2001, 2001–2002, and 2002–2003 grazing seasons: (1) ungrazed, released from grazing; (2) dry-season grazed, grazed October through November and mid-April through June; (3) wet-season grazed, grazed December through mid-April; and (4) continuously grazed, control, grazed during the historical grazing season (October through June). Electric fencing was used to exclude cattle from the ungrazed and seasonally grazed treatments. Cattle exclosures ranged in size from 0.33 to 0.80 ha, which included an average 14-m buffer around each pool and a 9:1 ratio of upland to pool area. Pool area and depth did not differ significantly among treatments at the beginning of the experiment.

I collected data on plant species composition each year in permanently marked 35 × 70 cm quadrats after the pools had dried and the majority of the plant species were flowering (April—May). Quadrats were randomly located and sampled along three transects for each pool in three different pool zones (3 quadrats × 3 zones = 9 quadrats per pool). The three zones were the (1) deepest part of the pool, (2) the edge of the pool (selected in the first year based on the high-water mark of the pool), and (3) upland area (5 m from the adjacent edge quadrat). Each plant species occurring in the quadrat was recorded and given a modified Daubenmire cover class value (Barbour et al. 1987). I pooled quadrat data for each zone in each pool. Cover class values were converted to midpoint cover values to calculate percent cover. I calculated relative cover of native species to assess the relative effect of grazing treatments on native species in relation to exotic species. Soil compaction was measured with a penetrometer (Geotest Instrument Corporation, Evanston, Illinois) at each of the vegetation sampling points ($n = 9$ per pool) in October 2003, before the first rainfall of the season.

Once the pools filled with water, I took weekly depth measurements at a permanent marker located in the deepest part of each pool. The weekly presence or absence of water was used to calculate total and maximum inundation period for each pool and the number of dry-down periods during the grazing season. In 2001 I did not start collecting data on pool depth until February, so period of inundation data are not available for the first season of the study.

I sampled for aquatic invertebrates once in January and once in March of each year in all pools that held sufficient water. In 2003 I also sampled a random subset of eight of the pools every 2 weeks until they were dry. I collected aquatic invertebrates and vertebrates in a D-shaped dipnet (500-μm mesh and 0.1-m^2 aperture). Each pool was proportionally sampled based on the surface area of water in the pool estimated in the first year of the study with a global positioning system (TSC1 Asset Surveyor, Trimble Navigation Limited, Sunnyvale, California) with submeter accuracy. I used the same sampling scheme throughout the study and adjusted it during pool dry down to reflect the reduced pool surface area. Ten percent of the area of each pool was sampled by sweeping the dipnet as close to the pool bottom as possible along a randomly located transect. The number of transects and length of each transect per pool were established in the first year of the study. For example, a 210-m^2 pool would receive seven, 3-m-long, randomly located dipnet sweeps. All contents collected in the net from a pool were consolidated and surveyed for threatened and endangered species before preserving the sample in 70% isopropyl alcohol. All threatened and endangered species were recorded, removed from the sample, and returned to the pool. Samples were stored at room temperature until they could be sorted and identified to the lowest taxonomic level in the laboratory. With only five exceptions ($n = 42$), all invertebrate taxa were identified at least to genus.

Statistical Analyses

I used a two-way, nested analysis of variance (ANOVA) model with experimental block and grazing treatments as main effects and pool nested within grazing treatment to test for significant nested effects for each variable measured in each year for all pool zones combined. If the nested effect was not significant, I pooled the data for each plot and then performed the statistical analysis with block and grazing treatment as main effects. I used repeated-measures multivariate analysis of variance (MANOVA) to test for treatment effects across years. For the vegetation data, I also tested for grazing effects within each pool zone separately. Pairwise comparisons were made with Tukey's honestly significant difference (HSD) test (Sokal & Rohlf 1994). Stepwise multiple regression analysis was used to determine the relationship between faunal richness and pool area and depth. I report diversity as species or taxa richness. All analyses were conducted using JMP statistical software (version 4.0, SAS Institute 2001).

Results

The continuously grazed (CG) pools had the highest relative cover of native species across all 3 years of the experiment ($n = 69$, $F = 10.54$, $p < 0.0001$). In 2001 the relative cover of natives was 20% higher in the CG treatment than in the ungrazed (UG) and dry-season grazed (DG) treatments ($n = 72$, $F = 5.50$, $p < 0.01$). In 2002 and 2003 relative native cover was 26 to 47% higher in the CG treatment than in the wet-season grazed (WG) and UG treatments ($n = 72$, 2002: $F = 7.01, p < 0.001$; 2003, $F = 10.12, p < 0.0001$). The effects of grazing on relative native cover in the pool zone were not significantly different in any of the 3 years. By 2003 relative native cover in CG treatments in the edge zone was 80% higher than in the UG treatment ($n = 24$, $F = 11.93$, $p < 0.001$) and 160% higher than in the UG treatment in the upland zone ($n = 24$, $F = 8.18$, $p < 0.01$, Fig. 1a).

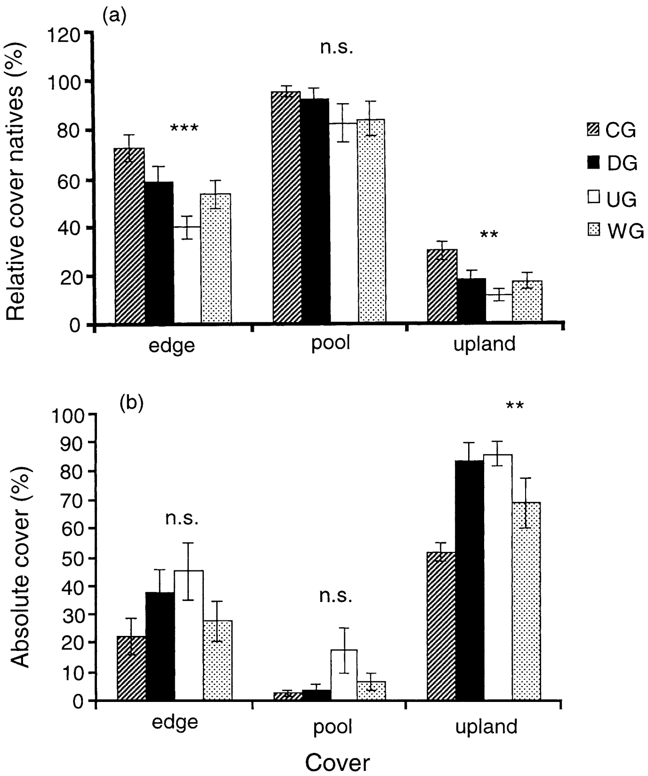

Figure 1. Effect of grazing treatments in three vernal-pool zones in 2003 on (a) relative cover of native species and (b) absolute cover of exotic annual grasses (CG, continuously grazed; DG, dry-season grazed; WG, wet-season grazed; UG, ungrazed; n.s., not significant; **p < *0.01,* ***p < *0.001).*

Exotic annual grass cover increased dramatically in the pools with grazing removal during the experiment (n = 69, F = 10.74, p < 0.0001). In 2001 exotic grass cover was 67% higher in the UG versus CG treatments (n = 72, F = 3.86, p = 0.01). In 2002 exotic grass cover was 60 to 130% higher in the UG treatment than in all other treatments (n = 72, F = 11.83, p < 0.0001). In 2003 the DG and UG treatments had 60 and 88% more exotic grass cover, respectively, than the CG treatment (n = 72, F = 7.76, p < 0.001). This effect was significant in the pool zone only in 2002 (n = 24, F = 3.30, p = 0.05) and in the upland zone in 2002 (n = 24, F = 14.78, p < 0.001) and 2003 (N = 24, F = 7.15, p < 0.01) but was not significant in the edge zone in any year (Fig. 1b).

I measured a strong increase in cover of grasses relative to forb cover in the ungrazed treatments (n = 69, F = 7.41, p < 0.001). The ratio of grass cover to forb cover was not significantly different among treatments in 2001 (n = 72, F = 2.10, p = 0.10) but was nearly two times higher in UG than in all other treatments in 2002 (n = 72, F = 4.29, p < 0.01) and three times higher in UG than in the CG treatment in 2003 (n = 72, F = 7.02, p < 0.001, Fig. 2). By 2003 the ratio was four times higher in UG

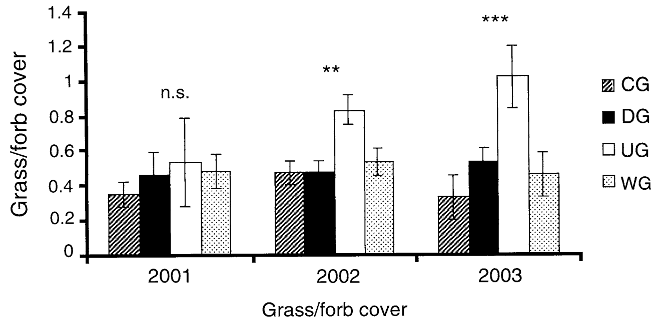

Figure 2. Effect of grazing treatments on the grass to forb cover ratio over the 3 years of the experiment (CG, continuously grazed; DG, dry-season grazed; WG, wet-season grazed; UG, ungrazed; n.s., not significant; **p < *0.01,* ***p < *0.001).*

pools than in CG pools (n = 24, F = 2.95, p = 0.06) and two to three times higher in UG and DG uplands than in CG uplands (n = 24, F = 4.85, p = 0.001).

Native plant species richness either increased or remained the same over the 3 years of the experiment in the CG, WG, and DG treatments, whereas it declined in the UG treatments (n = 72, F = 7.61, p < 0.001, Fig. 3). The change in native species richness in the pool zone was not significantly different among grazing treatments. In the edge zone, the UG pools had on average three fewer native species per quadrat than the CG pools (n = 24, F = 9.49, p < 0.001). The UG upland zone had one to two fewer native species per quadrat than the WG and CG uplands s. This change in diversity represented a loss of 25% of the average native species richness in the edge and upland zones over the 3 years of the experiment.

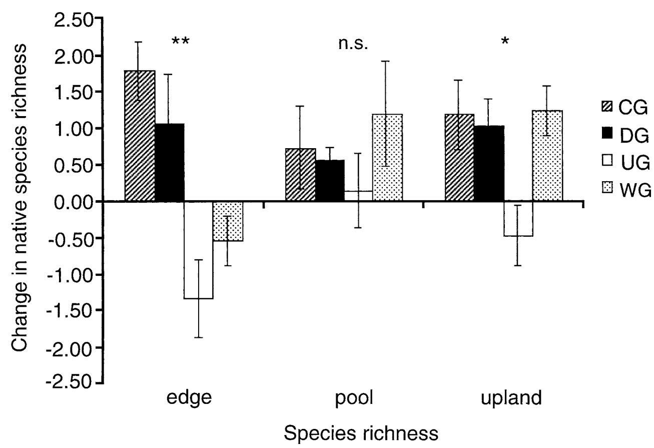

Figure 3. Change in native species richness (s) per quadrat between 2001 and 2003 in the four grazing treatments (CG, continuously grazed; DG, dry-season grazed; WG, wet-season grazed; UG, ungrazed; n.s., not significant; *p < *0.05,* **p < *0.01).*

In 2003 the CG pools had a total inundation period that was on average 49 days longer than the UG pools and 24 days longer than the WG pools ($n = 72$, $F = 7.30$, $p < 0.001$). More important, maximum inundation period in the CG pools was on average 115 ($\pm$ 9) days, whereas UG pools were inundated for an average of 65 ($\pm$ 8) days, DG pools for 78 ($\pm$ 7) days and WG pools were inundated for 65 ($\pm$ 8) days ($n = 72$, $F = 10.53$, $p < 0.0001$). The sporadic rainfall pattern in 2003 led to several of the pools drying and refilling during the rainy season. The CG pools dried on average less than one time during the season (0.61 $\pm$ 0.14 dry-down periods), whereas the UG, DG, and WG pools dried on average twice during the season (2.11 $\pm$ 0.25, 1.61$\pm$ 0.18, 1.67 $\pm$ 0.21 dry-down periods, respectively). Hydroperiod did not differ significantly among grazing treatments in 2002. Soil compaction was significantly lower in the UG treatment than in all other grazing treatments ($n = 72$, $F = 20.19$, $p < 0.001$). Compaction ranged from 3.88 $\pm$ 0.10 kg/cm^2 in the UG treatment to 4.48 $\pm$ 0.01 kg/cm^2 in the CG pools.

In 2003 the UG pools had the lowest invertebrate taxa richness with an average of 10 ($\pm$ 0.80) invertebrate taxa, whereas the CG, DG, and WG pools had an average of 14 ($\pm$ 0.50), 12 ($\pm$ 0.72), and 11 ($\pm$ 0.62) taxa, respectively ($n = 109$, $F = 3.41$, $p = 0.02$). Pool depth and period of inundation were the strongest predictors of total invertebrate taxa richness in 2003 ($n = 109$, $r^2 = 0.25$, $p < 0.0001$; $p = 0.03$, respectively). Taxa richness was not significantly different among treatments in 2001 or 2002.

Discussion

My field experiments indicate that when cattle are removed from grazed vernal pool grasslands, diversity declines and non-native species abundance increases. The decline in native plant cover and diversity in the ungrazed treatments was most likely caused by the significant increase in grass cover. Exotic grasses maintain dominance primarily by competing for soil moisture and light resources (Barbour et al. 1993) and accumulation of thatch (Huenneke et al. 1990). Many of the native vernal pool plants (e.g., *Lasthenia* spp., *Downingia* spp., *Veronica* spp.) are small and require an open environment to successfully germinate and reproduce (Linhart 1988). Cattle grazing may be particularly effective at reducing exotic grass cover because cattle selectively forage on grasses (Kie & Boroski 1996; Knapp et al. 1999) and help maintain a more open canopy (Weiss 1999).

Most of the exotic grasses in this system cannot tolerate extended periods of inundation, so hydrology plays a major role in controlling grass encroachment into the pools (Gerhardt & Collinge 2003). My results show, however, that prolonged inundation in the absence of grazing is not enough to keep exotics out of the pools. Moreover, the decreased inundation period in the pools may make the habitat more suitable for exotic grass growth and invasion. The edge and upland zones were the most negatively affected by grazing removal with marked declines in native species richness and relative cover of natives. The loss of native plant species diversity on the edge of the pool in particular may adversely affect other trophic levels such as specialist pollinators that depend on the pollen of the plants which grow only in that pool zone (Thorp & Leong 1998).

The primary cause of the dramatic decrease in pool hydroperiod in the ungrazed and seasonally grazed treatments may be increased evapotranspiration rates that resulted from the abundance of vegetation, principally grasses, in and around the pools. This conclusion is supported by studies in the Midwest and northern Great Plains that documented higher evapotranspiration rates in ungrazed grasslands relative to grazed grasslands (Bremer et al. 2001; Frank 2003). Results from studies in other habitats show significant negative effects of abundant vegetation on hydrology in wetlands and streams (Bliss & Comerford 2002; Moorhead 2003).

Although decreased soil compaction in UG pools does not appear to be a major factor in reducing inundation period, I cannot rule out changes in the water-holding capacity of the soil as a contributing factor. The pattern of water depths for 2003 in the pools showed little difference between grazed and ungrazed pools during the initial inundation period, but a sharp decline in depth quickly followed by complete drying in the ungrazed pools occurred once the primary vegetation growth period began in early March (J.T.M., unpublished data). If decreased soil compaction was a major contributing factor, then the hydrology in the UG pools should have differed significantly throughout the season rather than just at the end of the season.

It is important to remember that this is a relatively short-term study in a system driven by variable rainfall and temperature regimes. I expect the effects of grazing removal on vernal pool hydrology to be less prominent in years with consistent, above-average rainfall and in areas with much higher and much lower annual rainfall than my study site (Pyke & Marty 2005).

The decline in invertebrate taxa richness in the ungrazed pools was most likely due to the altered pool hydrology, particularly the increased number of dry-down periods. Pools with shorter hydroperiods tend to be inhabited by species with rapid development cycles, mainly because the pools dry up before longer-lived species are able to complete their life cycles (King et al. 1996). Although the invertebrate communities in all the study pools developed quickly, reaching maximum taxa richness approximately 6 weeks after first inundation for all treatments (J.T.M., unpublished data), each dry and refill cycle in the UG pools essentially arrested community development, therefore contributing to a lower number of taxa in the next sampling cycle. The invertebrate communities in the continuously grazed pools had sufficient time to develop and presumably provide for the successful growth and reproduction of the longer-lived taxa.

In addition to negatively affecting community diversity, this shift in hydrology has important implications for the individual species that inhabit these pools. In particular, the decreased hydroperiod in the ungrazed and seasonally grazed pools may not support the long reproductive cycles of some of the rare invertebrate and vertebrate species that depend on these pools to complete their life cycles. For example, California tiger salamanders (*Ambystoma californiense*) require pools with continuous inundation periods of 70–90 days (Shaffer & Trenham 2004). The Western spadefoot toad (*Spea [Scaphiopus] hammondii*) that inhabits these vernal pools could be negatively affected by hydroperiod reduction. They require pools with on average 80 days of inundation (Morey 1998). The ungrazed pools in my study could not provide suitable toad and salamander habitat, and the seasonally grazed pools could provide only marginal habitat.

Why is cattle grazing so clearly beneficial to biodiversity in these vernal pools, when conservationists often advocate severe grazing restrictions? The answer to this question comes in part from the fact that California grasslands have a long history of extensive grazing dating back to the Pleistocene but were most recently grazed by herds of tule elk (*Cervus elaphus nannodes*) and pronghorns (*Antilocarpa americana*) before livestock introduction in the late 1800s (Edwards 1996). Hence, the pool species are adapted to some level of grazing. In addition, the plant species composition of California Central Valley grasslands has changed significantly since European settlement and is now dominated by exotic annual grasses (Barbour et al. 1993). Thus, a long history of grazing coupled with the altered plant community yields a system that is now adapted to the changes brought about by cattle and one that becomes quickly degraded when cattle are removed.

Conclusion

The conservation of rare habitats and the species that rely on them depends not only on staving off development but also on implementing appropriate management regimes. It is not enough to simply monitor change in these systems as we guess at what the appropriate management formula might be. Experimental studies testing a variety of management options are the best hope for successful conservation. In the vernal pool grasslands I studied, I found that livestock grazing played an important role in maintaining species diversity. There were significant negative effects on the native plant community, pool hydrology, and the aquatic invertebrate community with the removal of grazing. Grazing should be considered one of a variety of important tools for land managers interested in the maintenance of biodiversity. The debate over grazing needs to move beyond the simple dichotomy of whether it is good or bad and be properly evaluated through experimental studies of practical alternatives.

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